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Disturbance-mediated facilitation by an intertidal ecosystem engineer

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Abstract. Ecosystem engineers facilitate communities by providing a structural habitat that reduces abiotic stress or predation pressure for associated species. However, disturbance may damage or move the engineer to a more stressful environment, possibly increasing the importance of facilitation for associated communities. In this study, we determined how disturbance to intertidal boulders (i.e., flipping) and the subsequent movement of a structural ecosystem engineer, the tube-forming serpulid worm *Galeolaria caespitosa*, from the bottom (natural state, low abiotic stress) to the top (disturbed state, high abiotic stress) surface of boulders influenced the importance of facilitation for intertidal communities across two intertidal zones. Theory predicts stronger relative facilitation should occur in the harsher environments of the top of boulders and the high intertidal zone. To test this prediction, we experimentally positioned boulders with the serpulids either face up or face down for 12 months in low and high zones in an intertidal boulder field. There were very different communities associated with the different boulders and serpulids had the strongest facilitative effects on the more stressful top surface of boulders with approximately double the species richness compared to boulders lacking serpulids. Moreover, within the serpulid matrix itself there was also approximately double the species richness (both zones) and abundance (high zone only) of small invertebrates on the top of boulders compared to the bottom. The high relative facilitation on the top of boulders reflected a large reduction in temperature by the serpulid matrix on that surface (up to 10°C) highlighting a key role for modification of the abiotic environment in determining the community-wide facilitation. This study has demonstrated that disturbance and subsequent movement of an ecosystem engineer to a more stressful environment increased the importance of facilitation and allowed species to persist that would otherwise be unable to survive in that environment.

Key words: abiotic stress; boulder-field; disturbance; ecosystem engineering; facilitation; Galeolaria caespitosa; *intertidal; serpulid; tube worm.*

Introduction

Ecosystem engineers have major effects in ecosystems by altering resource availability, modifying the abiotic environment and changing food webs (Jones et al. 1997, Hastings et al. 2007). The facilitative effects of autogenic ecosystem engineers or foundation species (Dayton 1972) can be extensive. In situations where they add physical habitat to ecosystems that lack structure, such as bare sand, soil or rock; entire communities that are unable to exist without the engineer are facilitated (Cavieres et al. 2007, Silliman et al. 2011, Byers et al. 2012). There are several mechanisms by which the facilitation of communities can occur (Crooks 2002, Bruno et al. 2003) including a reduction in abiotic stress and predation pressure for associated species and the provision of space for attachment (Gribben et al. 2009, Altieri et al. 2010, Wright et al. 2014). In many situations amelioration of abiotic stress is critical (e.g., Silliman et al. 2011). Importantly, the strength of a species as a facilitator often varies across environmental gradients, and engineers that ameliorate abiotic stress have strong community-level effects in harsh environments enabling species that would otherwise be excluded by abiotic stress to persist (Bertness and Callaway 1994, Crain and Bertness 2006, Brooker et al. 2008).

Disturbance to an ecosystem engineer will have large implications for facilitated communities if the abiotic conditions and resources it modifies change. In some situations, disturbance might actually move an ecosystem engineer from one place to another, creating opportunities for facilitation in a different environment. For example, disturbance from storms can break and move mussels (Reusch and Chapman 1995) and corals (Smith and Hughes 1999) while refloated drift-ice can move salt marsh and mussels (Bertness and Grosholz 1985). In these situations, the engineers are deposited elsewhere where they can reattach, survive and function. Movement

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of ecosystem engineers also occurs if they are attached to another structure that is moved by a disturbance, such as epiphytes attached to a tree (Matelson et al. 1993) or seaweed and invertebrates attached to boulders (McGuinness 1988) or bivalve shells (Gribben et al. 2009). In the case of some structural engineers, the engineering effects may still occur even when the engineer does not survive the disturbance because the structure of the engineer remains intact (Hastings et al. 2007, Jones et al. 2010). In marine systems, such examples might include oysters or mussels that are detached from the substratum and relocated where the engineering of abiotic factors by the structure of the shell remains. Because theory predicts the importance of facilitation will increase with increasing environmental stress, disturbances that result in the movement of engineers to more stressful environments should allow associated species to survive in environments where they are typically excluded.

Marine intertidal ecosystem engineers such as saltmarsh, seaweed, mussels and oysters facilitate invertebrate communities by reducing abiotic stresses such as temperature and desiccation at low tide, minimizing wave energy or by providing a refuge from predation (Bertness et al. 1999, Bruno 2000, Altieri et al. 2010, Kimbro et al. 2014, Wright et al. 2014). Moreover, intertidal ecosystem engineers can have stronger facilitative effects higher up the shore where high zones are exposed to extremes of temperatures and humidity for longer (Bertness et al. 1999, Watt and Scrosati 2013). In intertidal boulder fields, ecosystem engineers such as mussels and seaweed attach to the top of boulders while polychaetes, sponges and bryozoans attach to the bottoms (Sousa 1979, McGuinness 1987, 1988). In addition, a diverse assemblage of small mobile invertebrates are associated with these ecosystem engineers (Chapman 2005, 2012, Wright et al. 2016). The disturbance to boulders by waves (Sousa 1979) results in the redistribution of the ecosystem engineers from the top to the bottom of the boulder or vice versa. Some of these engineers from the bottom of boulders will not survive in the harsher conditions on the top of boulders where light, temperature and desiccation stress will be higher. However, calcareous structures such as the shells of bivalves and barnacles and the tubes of polychaetes often remain attached to the top of boulders long after the ecosystem engineer has died (personal observations). In these circumstances, the structural properties of the engineer and modification of abiotic factors can still occur, providing shelter for species that would otherwise not survive there (Summerhayes et al. 2009, Harley and O'Riley 2011).

In southeastern Australia, the undersides of intertidal boulders are often covered (up to 100% cover) by a matrix of tubes from the habitat-forming serpulid *Galeolaria caespitosa* (Gribben et al. 2015, Wright et al. 2016). This matrix is made up of hundreds of small tubes approximately ~30 mm in length (Halt et al. 2009) which creates a highly complex microstructure with many small crevices and interstices (Fig. 1). When this matrix is on the underside of boulders it facilitates the recruitment of intertidal invertebrates (Wright et al. 2016), possibly by providing greater habitat complexity than bare boulders that enhances attachment under

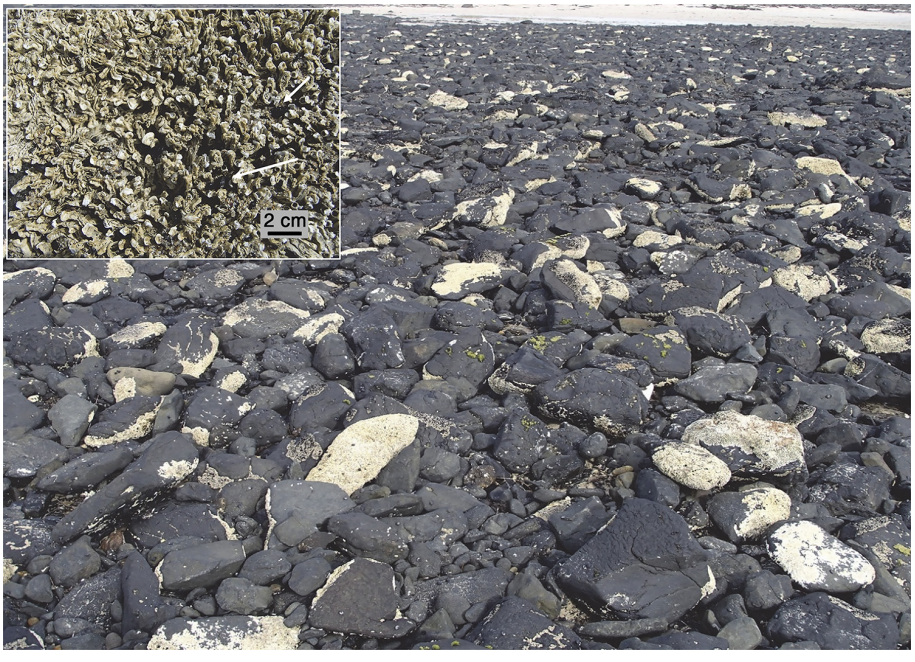

FIG. 1. Intertidal boulder field at Bell Buoy Beach showing numerous boulders with the serpulid matrix face-up. Inset: close-up of the calcareous matrix formed by the serpulid *Galeolaria caespitosa* on intertidal boulders. *Limnoperna pulex* (arrows) can be seen within the matrix.

wave buffering or reduces abiotic stresses and consumer pressure. When boulders in this system are flipped over by waves, the tube worm matrix remains on the top of the boulders, although the worms do not survive. Thus, there is a mosaic of three different types of boulders in these boulder fields: boulders with serpulids on their bottom surface, boulders with serpulids on their top surface and boulders without serpulids (Fig. 1).

In this study, we determined how disturbance to boulders and movement of the ecosystem engineering serpulid influenced the facilitation of intertidal communities. Although marine ecosystem engineers can be moved by disturbance, we know little about the consequences of this movement for associated communities and, in particular, how the facilitative effects might differ across stress gradients if the engineer is moved to a more stressful environment. Here, we hypothesized there would be stronger relative facilitative effects by serpulids in the harsher environments of the top vs. bottom of boulders and the high vs. low intertidal zone where organisms are exposed to longer periods of emersion stress. To test these hypotheses, we experimentally positioned boulders with the serpulids either face up or face down for 12 months in low and high zones and asked the following questions: (1) Does the entire intertidal community associated with boulders (top and bottom communities combined), the bottom community only and the top community only differ among the three different boulder types (serpulids on the bottom surface only, serpulids on the top surface only and bare boulders with no serpulids on either surface) and between low and high zones? Given the small size of serpulids it may be that only the small invertebrates that live within the serpulid matrix might be affected. Thus, we also asked: (2) Do invertebrate communities that live within the serpulid matrix itself differ depending on whether the serpulids are on the top or bottom of the boulder and between zones? In addition, the four boulder treatments with serpulids create a gradient of increasing stress from low zone/bottom of boulder → high zone/bottom of boulder → low zone/top of boulder → high zone/top of boulder, suggesting that relative facilitation of community structure (e.g., species richness or abundance) should also increase along this gradient. Consequently, we also asked: (3) Does the relative importance of facilitation of the total boulder community and the matrix community increase from the least to most stressful conditions? Finally, to understand the mechanism promoting the facilitation we determined the reduction in temperature due to the presence of serpulids on boulders.

Materials and Methods

Study system

This study was undertaken on the northern coast of Tasmania, southern Australia. Intertidal rocky shores in this region are semi to fully exposed and are typically characterized by relatively low wave energy and low vertical relief boulder fields (Gribben et al. 2013, 2015). The boulders on these shores vary in size but reach up to 2,000 cm^2 (bottom surface area, J. T. Wright, *unpublished data*). In addition to a matrix of serpulids on the underside of boulders, there is a diverse assemblage of invertebrates beneath boulders dominated by native chitons, gastropods and crabs, and the invasive New Zealand porcelain crab, *Petrolisthes elongatus* (Gribben et al. 2015). At many sites there are boulders with the serpulid matrix on the top surface indicating disturbance to these boulders by waves. Boulders with no serpulids on either surface are typically only found in very high zones.

Facilitation of communities on upper and lower surface of boulders

To determine the role of serpulids in facilitating communities on the top and underside side of boulders, an experiment was set up in February 2015 at Bell Buoy Beach (41°02′25″ S, 146°49′58″ E). There were three treatments: boulders with serpulids on the top surface only (hereafter serpulid-up), boulders with serpulids on the bottom surface only (hereafter serpulid-down) and boulders with no serpulids on either side (hereafter bare). To address whether facilitation differed as a function of emersion time, we established the experiment in two zones hereafter called the low (~0.7 m) and high (~1.2 m) zones with $n = 8$ boulders per treatment per zone. Experimental boulders were selected haphazardly from the boulder field at Bell Buoy Beach but we ensured that all boulders in the serpulid treatments had at least 70% cover of serpulids ($87.3 \pm 1.6\%$, mean ± SE, $N = 32$ boulders, pooled across zones) while the no-serpulid side of all boulders had no or very low serpulid cover ($2.6 \pm 0.6\%$, mean ± SE, $N = 64$, pooled across zones). All boulders were examined to ensure they did not have any other habitat-forming species on them (e.g., mussels, algae, barnacles) and all visible mobile species were removed. Small invertebrates occur within the serpulid matrix but we were unable to remove these without destroying the matrix. The top and bottom surface of each boulder were photographed and the surface area and initial percentage cover of serpulids determined using ImageJ. Boulder size varied but all boulders were within a size range of 500–1,600 cm^2. After the experiment was established and photos were processed, we found that bare boulders were significantly smaller than both serpulid-up and serpulid-down boulders in both zones (bottom of boulders: $F = 14.454$, $P < 0.001$, top of boulders: $F = 12.051$, Tukey's tests, both $\alpha < 0.05$: bare < serpulid-up = serpulid-down). The mean ± SE surface area of the top of boulders was bare: 688.6 ± 42.0 cm^2, serpulid-up: 982.7 ± 43.9 cm^2, serpulid-down: $1{,}003.6 \pm 58.6$ cm^2. The mean ± SE surface area of the bottom of boulders was bare: 721.1 ± 44.0 cm^2, serpulid-up: 939.8 ± 41.2 cm^2, serpulid-down: $1{,}083.2 \pm 53.4$ cm^2).

Boulders were haphazardly positioned at least 1 m apart along ~30 m transects running parallel to the

shore in each zone. We minimized the possibility of the experimental boulders moving in the waves by ensuring they were placed relatively flat on the bedrock and/or by removing an existing boulder and replacing it with the experimental boulder. To aid in identification a dot (~3 cm diameter) was painted on 2–3 sides of each experimental boulder and their position along the transect was recorded. During the experiment six boulders flipped over or moved and thus were excluded resulting in N = 6 replicates for the serpulid-up/high zone and serpulid-down/low zone treatments; N = 7 replicates for the serpulid-up/low zone and control/low zone treatments and; N = 8 replicates for the serpulid-down/high zone and control/high zone treatments at the end of the experiment. Although we tried to minimize boulder movement to isolate the treatment effects, the movement of 12.5% of our experimental boulders over a year is consistent to boulder movement at a nearby site where 34% of permanent quadrats experienced boulder movement over a 2-yr period (R. D. Lewis, *unpublished data*).

After 12 months, communities on both the top and bottom of boulders were sampled. To quantify communities on the top of boulders, mobile invertebrates were identified and counted in situ and a photo taken of the surface to determine the percentage cover of serpulids and abundance of barnacles. Communities on the bottom of boulders were quantified as in Gribben et al. (2013, 2015). Briefly, for the bottom community, mobile invertebrates beneath each boulder were collected by hand, stored in 70% ethanol and counted back in the lab. Photographs were also taken of the underside of all boulders and the surface area of all serpulids was quantified. In addition, for each boulder with the serpulid matrix, one 6 cm × 6 cm quadrat of the serpulid matrix was removed from the centre of the matrix by cutting through it to the boulder surface with a chisel. The contents of the quadrat were placed into 70% ethanol and densities of species within the matrix were counted back in the lab under a dissecting microscope.

Relative facilitation

To assess the relative facilitation by serpulids under different conditions of stress we conducted two further analyses separately for the matrix and non-matrix communities. For the non-matrix community, we compared the percentage change in species richness and total invertebrate abundance in the serpulid-up and serpulid-down boulders relative to bare boulders. We compared the community on the top of serpulid-up boulders to the community on the top of bare boulders and the community on the bottom of serpulid-down boulders to the community on the bottom of bare boulders, separately for each zone. To do this, we first calculated the mean richness and abundance on bare boulders, determined the percentage change in these metrics for each serpulid boulder and then calculated the mean percentage change and confidence intervals around that mean. Confidence intervals above zero indicate significant facilitation in a given environment, confidence intervals overlapping with zero indicate no facilitation while confidence intervals below zero indicate inhibition.

For the community within the serpulid matrix, we compared the percentage change in species richness and total invertebrate abundance on the top of boulders to the less stressful bottom of boulders. Here, we first calculated the mean richness and abundance in the serpulid matrix of the serpulid-down boulders (separately for each zone), determined the percentage change in these metrics for each serpulid-up boulder and calculated the mean percentage change and confidence intervals around that mean. Confidence intervals above zero indicate significant facilitation of the matrix community on the top of boulders.

Temperature amelioration by serpulids

Temperature amelioration by serpulids was determined by measuring the surface temperature on the top and bottom of serpulid-up and serpulid-down boulders in the low and high zones (N = 10 rocks of each type in each zone). We used a Digitech infra-red thermometer (model QM7215) which measures temperature to within 0.1°C. The infra-red sensor was positioned a standard distance from the surface (25–30 mm) each time with measurements done three times over 90 min on a sunny, warm day (ambient temperature ranged from 18° to to 28.3°C, 22.4 ± 0.5, mean ± SE). Three measurements were taken over 90 min to determine whether temperature increased as exposure time increased. Each measurement was done on a different boulder. Measurements on the bottom of boulders were done immediately upon turning the boulder over to avoid the surface heating up.

Analyses

We analyzed the total community (top and bottom communities combined), bottom community only, top community only and matrix community (the matrix community was not included in the other analyses) separately. All counts for total, bottom and top communities were corrected for boulder surface area prior to analysis with a 2-Factor permutational multivariate ANOVAs (PERMANOVAs) with the factors zone (low and high) and boulder type (serpulid-up, serpulid-down and bare) as categorical variables. For the top community, we removed three rocks that had no community members from the analysis (the result of the PERMANOVA did not change but removing these three rocks allowed the nMDS to be interpreted). The matrix community was analyzed using a 3-Factor PERMANCOVA (serpulid position; top or bottom of the rock, zone and the surface area of serpulids on the rock as a covariate) on non-standardized data as we sampled the same area each time but we included the area of serpulids as a covariate to determine if it influenced the invertebrate community

living within the matrix. All PERMANOVAs used 9,999 permutations of Bray Curtis similarities on square root transformed data and Type III sums of squares. Non-significant interaction terms ($P > 0.25$) were pooled with the Residual to increase the power of tests for other terms in the model. Results for the PERMANOVAs were explored graphically using nMDS and SIMPER was used to identify the variables explaining most of the variation among factors. All multivariate analyses were conducted using PERMANOVA+ and PRIMER packages (Clarke and Gorley 2006; Anderson et al. 2008).

Univariate analyses of variance (ANOVA) were then used to determine differences between zone and boulder type in total invertebrate abundance, species richness and the abundance of the species contributing most to the multivariate patterns (based on SIMPER) separately for the total community, bottom community and top community. Differences in total invertebrate abundance, species richness and the abundance of the species contributing most to the multivariate patterns within the serpulid matrix were determined using 3-Factor ANCOVAs (serpulid position; top or bottom of the rock, zone with the surface area of serpulids on the rock as a covariate). For all univariate analyses, data were transformed as necessary to meet ANOVA assumptions and interactions were removed where $P > 0.05$. The abundance of some individual species (both matrix and non-matrix communities) was often highly skewed with zero or very low abundance in some treatments. We did not formally analyze these species but highlight them in the text.

We determined differences in the temperature of the top and bottom surfaces separately with a 3-factor ANOVAs (with and without serpulids × zone × time). We also calculated the difference in surface temperature between boulders with and without serpulids separately for each boulder surface (top and bottom) in each zone at each of the three times (0, 30 and 90 min). To do this, we randomly paired boulders with and without serpulids and calculated the difference in temperature between each pair via subtraction.

Results

Total communities

The three different types of boulder had very different total invertebrate communities (top and bottom of boulders combined) associated with them with significant differences in community structure among boulder types (Pseudo-$F_{2,36} = 1.321$, P(perm) < 0.001) and between zones (Pseudo-$F_{1,36} = 4.390$, P(perm) < 0.001, Fig. 2A). The main species contributing to differences between serpulid-up and other treatments were the chiton *Sypharochiton pelliserpentis* (mostly found on the bottom of boulders) and the shell-less gastropod *Onchidella nigricans* (mostly found on the top of boulders) which were both more abundant in the serpulid-up treatment and *Petrolisthes elongatus* (only found on the bottom of boulders but did not differ in abundance between treatments Fig. 2A, Appendix S1). The main species contributing to differences between serpulid-down and bare boulders were *Petrolisthes* (only found on the bottom of boulders), barnacles (largely found on the bottom of boulders), and the keyhole limpet *Montfortula rugosa* and the whelk *Haustrum vinosa* (mostly on bottom of boulders). These latter two species were both more abundant in the serpulid-down treatment.

The combined abundance of invertebrates did not differ significantly among boulder types or zones (boulder type: $F_{2,38} = 0.868$, $P = 0.428$; zone: $F_{1,38} = 2.411$, $P = 0.129$) and the species richness was different among boulder type but not zone (boulder type: $F_{2,38} = 4.681$, $P = 0.015$; zone: $F_{1,38} = 0.184$, $P = 0.670$, Fig. 3). Species richness was significantly higher for bare rocks compared to serpulid-down rocks but there was no difference between serpulid-up and the other two treatments (Fig. 3).

Communities on the top of boulders

The top surface of the serpulid-up boulders had very distinct communities compared to the other two treatments (Pseudo-$F_{2,33} = 4.390$, P(perm) < 0.001, Fig. 2B). This separation of the serpulid-up treatment was most strongly correlated with a high abundance of *Onchidella* on all serpulid-up boulders in the low zone (14.1 ± 3.7 per boulder, mean ± SE) but which were largely absent from the top surface of boulders without serpulids, and a significantly lower abundance of *Nerita atramentosa* on serpulid-up boulders compared to bare boulders in the low zone (zone × boulder type interaction: $F_{2,36} = 10.286$, $P < 0.001$, Tukeys $\alpha < 0.05$, Appendix S1). The tops of the serpulid-up boulders had a significantly higher species richness compared to both other treatments (boulder type: $F_{2,36} = 11.395$, $P < 0.001$, Tukeys $\alpha < 0.05$) but similar total invertebrate abundance (Tukeys $\alpha > 0.05$, Fig. 3). The serpulid-down and bare boulders also had a different community structure which was strongly correlated with the higher abundance of *Nerita* (Tukeys $\alpha < 0.05$) and barnacles (not analyzed) on bare boulders (Fig. 2B). The bare boulders also had a higher total invertebrate abundance compared to serpulid-down boulders (boulder type: $F_{2,36} = 4.414$, $P = 0.019$, Tukeys $\alpha < 0.05$, Fig. 3) but did not differ in species richness (Fig. 3). Communities on the top of boulders also differed between zones (Pseudo-$F_{1,33} = 11.648$, P(perm) < 0.001, Fig. 2B) and the low zone had both a higher species richness ($F_{1,38} = 11.431$, $P = 0.002$) and abundance of invertebrates ($F_{1,36} = 48.203$, $P < 0.001$, Fig. 3) compared to the high zone.

Communities beneath boulders

Similar to the communities on tops of boulder, communities beneath the three types of boulders were also significantly different (Pseudo-$F_{1,38} = 5.631$, P(perm) < 0.001,

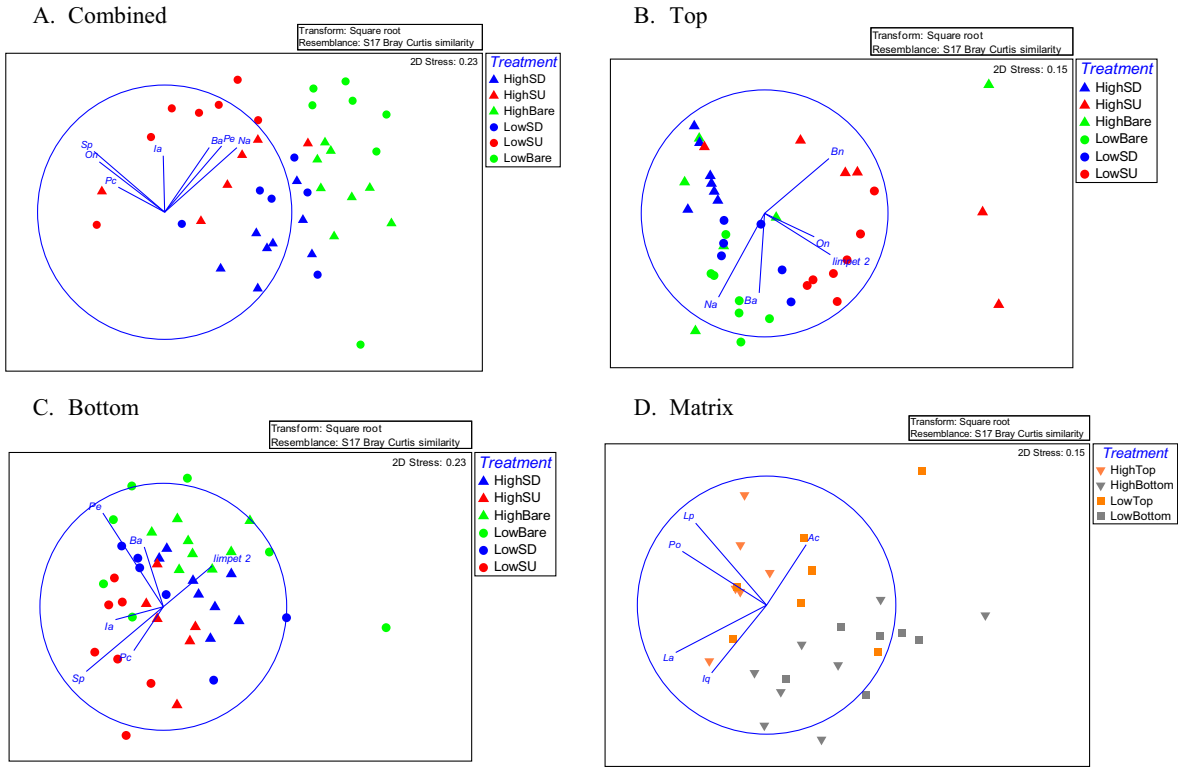

FIG. 2. Variation in invertebrate communities as a function of boulder type: serpulid-up (SU), serpulid-down (SD) and Bare in high and low zones. A (top and bottom communities combined), B (community on the top of boulders); and C (community on the bottom of boulders). D (community living within the serpulid matrix for SU and SD only). Ac, *Austrocochlea concamerata;* Ba, Barnacles; Bn, *Bembecium nanum;* Ia, *Ischnochiton australis;* Iq, *Ibla quadrivalvis;* La, *Lasaea australis;* Lp, *Limnoperna pulex;* limpet 2, unidentified limpet; Na, *Nerita atramentosa;* Oc, *Onchidella nigrescens;* Pe, *Petrolisthes elongatus;* Pc, *Patiriella calcar;* Po, polychaetes; Sp, *Sypharochiton pelliserpentis.*

Fig. 2C). The separation of the serpulid-up boulders from the other two boulder types reflected differences in the abundance of several species. The chiton *Sypharochiton* was more abundant beneath serpulid-up boulders compared to serpulid-down and bare boulders ($F_{2,38} = 29.262$, $P < 0.001$, Tukeys $\alpha < 0.05$), while the keyhole-limpet *Montfortula* and the whelk *Haustrum* were more abundant beneath serpulid-down boulders compared to serpulid-up and bare boulders (*Montfortula*: $F_{2,36} = 12.519$, $P < 0.001$, Tukeys $\alpha < 0.05$; *Haustrum*: $F_{2,38} = 6.844$, $P = 0.003$, Tukeys $\alpha < 0.05$, Appendix S1). The abundance of *Petrolisthes* did not differ between boulder type ($F_{2,38} = 1.315$, $P = 0.209$) or zone ($F_{1,38} = 0.042$, $P = 0.840$). The serpulid-down and bare boulders also had a different community structure beneath them (Fig. 2C). Community structure beneath boulders differed between zones and appeared to reflect differences in composition and not differences in species richness or abundance which did not differ among boulder type or zone (richness, boulder type: $F_{2,36} = 2.989$, $P = 0.063$; zone: $F_{1,36} = 1.733$, $P = 0.196$; abundance, boulder type: $F_{2,38} = 1.180$, $P = 0.318$; zone: $F_{1,38} = 0.230$, $P = 0.634$).

Communities within the serpulid matrix

A number of small invertebrate species that occurred within the serpulid matrix were never observed on boulders without serpulids including the mussel *Limnoperna pulex*, the stalked barnacle *Ibla quadrivalvis*, the bivalve *Lasaea australis* and small mobile polychaetes. Communities within the serpulid matrix differed between position (top or bottom of boulders, Pseudo-$F_{1,23} = 6.914$, $P(perm) < 0.001$), zone (Pseudo-$F_{1,23} = 2.437$, P(perm) = 0.033) and with the surface area of the serpulid on the boulder (Pseudo-$F_{1,23} = 3.359$, P(perm) = 0.008). There was a clear separation in communities depending on whether the serpulid matrix was on the top vs. the bottom of boulders (Fig. 2D) which largely reflected differences in the abundance of *Limnoperna,* several mobile species (*Onchidella* and polychaetes, Fig. 4), *Ibla* and *Lasaea* (Appendix S1). *Limnoperna* only occurred on the top of boulders and was significantly more abundant in the high zone ($F_{1,10} = 6.047$, $P = 0.034$) while mobile species (all species pooled) were significantly more abundant on the top of boulders ($F_{1,23} = 15.625$, $P < 0.001$) but did not differ between zones ($F_{1,23} = 0.459$,

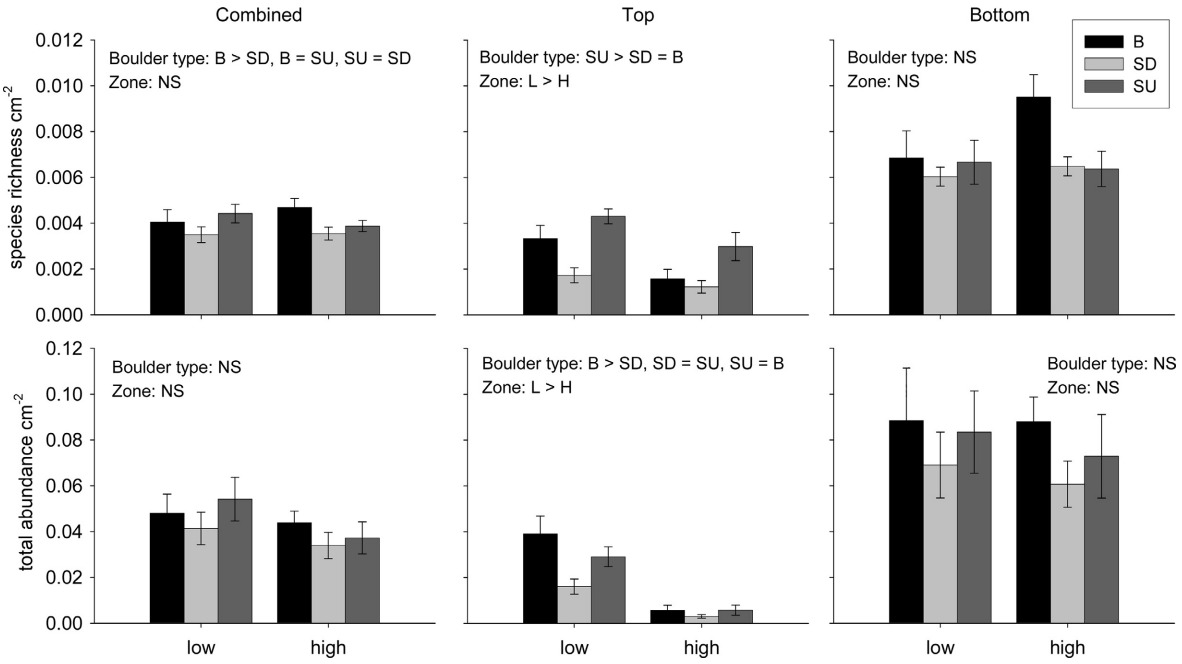

FIG. 3. Mean (± SE) species richness and the total abundance of invertebrates for the top and bottom communities combined, top community and bottom community among boulder type and zone (high and low zones). Result of Tukey's tests are shown. Boulder type abbreviations: bare (B), serpulid down (SD) and serpulid up (SU). NS, non-significant.

$P = 0.505$, Fig. 4). In contrast, the abundance of *Ibla* did not differ between the top and bottom of boulders ($F_{1,23} = 0.247$, $P = 0.624$) but was higher in the high zone ($F_{1,23} = 4.39$, $P = 0.047$) while *Lasaea* did not differ with position ($F_{1,23} = 0.231$, $P = 0.635$) or zone ($F_{1,23} = 2.477$, $P = 0.129$). Both total invertebrate abundance ($F_{1,22} = 10.361$, $P = 0.004$) and species richness ($F_{1,23} = 32.884$, $P < 0.001$) within the serpulid matrix were higher when the serpulid matrix was on the top vs. bottom of the boulder (Fig. 4). Total invertebrate abundance in the matrix was also significantly higher in the high vs. low zone ($F_{1,22} = 12.424$, $P = 0.002$) but species richness did not differ between zones ($F_{1,23} = 0.151$, $P = 0.701$, Fig. 4).

Relative facilitation across stress gradients

The relative importance of facilitation of the total (non-matrix) community species richness was higher on the top of boulders than beneath boulders in both zones (Fig. 5). Facilitation of total invertebrate abundance did not vary between the top and bottom of boulders or between zones. Serpulids appeared to inhibit species richness and total invertebrate abundance beneath boulders in the high zone (Fig. 5). Within the serpulid matrix, facilitation of species richness was relatively more important on the top of boulders and did not differ between zones while facilitation of invertebrate abundance was relatively important on the top of boulders in the high zone but not the low zone (Fig. 5).

Temperature amelioration

The serpulid matrix resulted in a large reduction in temperature on the top of boulders and also a reduction in temperature beneath boulders (Fig. 6). For the tops of boulders, the surface temperature with serpulids was significantly cooler than boulders without serpulids ($F_{1, 111} = 626.307$, $P < 0.001$) and temperature differed between zones although this interacted with time ($F_{2, 111} = 9.040$, $P < 0.001$). At all three times in both zones, the top of boulders with serpulids were ~7–10°C cooler compared to boulders without serpulids (initial temperature: 17.9 ± 0.5° vs. 24.8 ± 0.7°C in the high zone; 15.6 ± 0.3° vs. 24.8 ± 0.7°C, in the low zone; 30 min: 21.0 ± 1.0° vs. 29.9 ± 0.6°C in the high zone; 20.2 ± 1.0° vs. 29.1 ± 0.5°C, in the low zone; 90 min: 23.3 ± 0.8° vs. 33.8 ± 0.6°C in the high zone; 25.0 ± 0.6° vs. 35.5 ± 0.6°C, in the low zone; means ± SE, all N = 10).

The surface temperature on the bottom of boulders was more variable than the top with a significant zone × serpulid (presence/absence) × time interaction ($F_{2, 108} = 4.850$, $P < 0.010$). Although generally serpulids reduced temperature on the bottom of boulders (Fig. 6), the only differences between boulders with vs. without serpulids on the bottom within the same zone occurred in the high zone at 30 min (serpulids [18.0° ± 0.8°C] < no serpulids [24.4° ± 0.7°C], Tukey's $\alpha < 0.05$) and in the low zone at 90 min (serpulids [18.9° ± 0.6°C] <no serpulids [23.6° ± 0.9°C, means ± SE], Tukeys $\alpha < 0.05$).

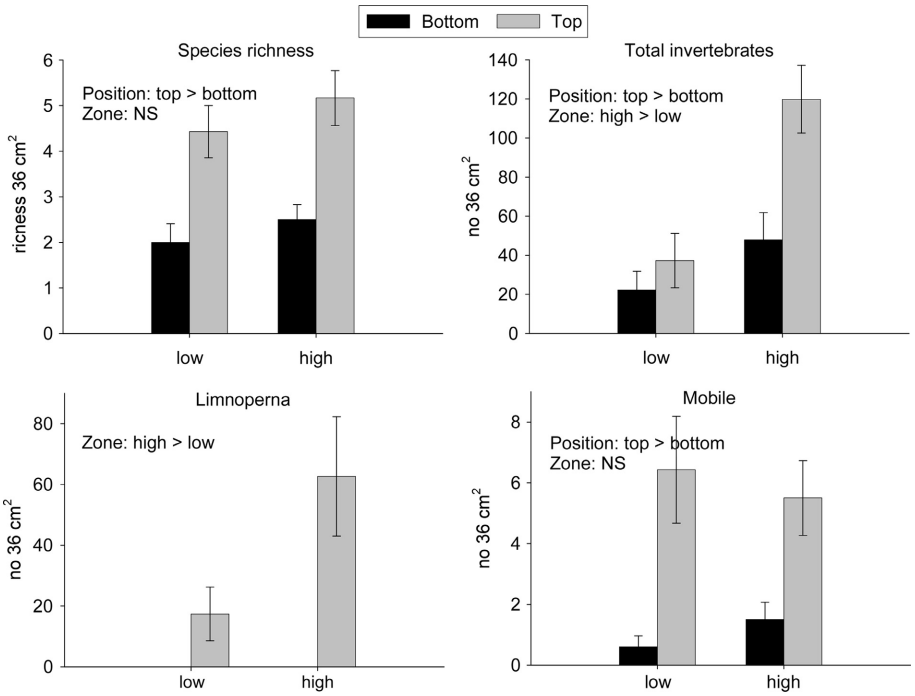

FIG. 4. Mean (± SE) species richness, total abundance, abundance of *Limnoperna pulex* and mobile species (pooled) within the serpulid matrix between the position of the serpulid matrix (top or bottom of boulders) and zone (low or high).

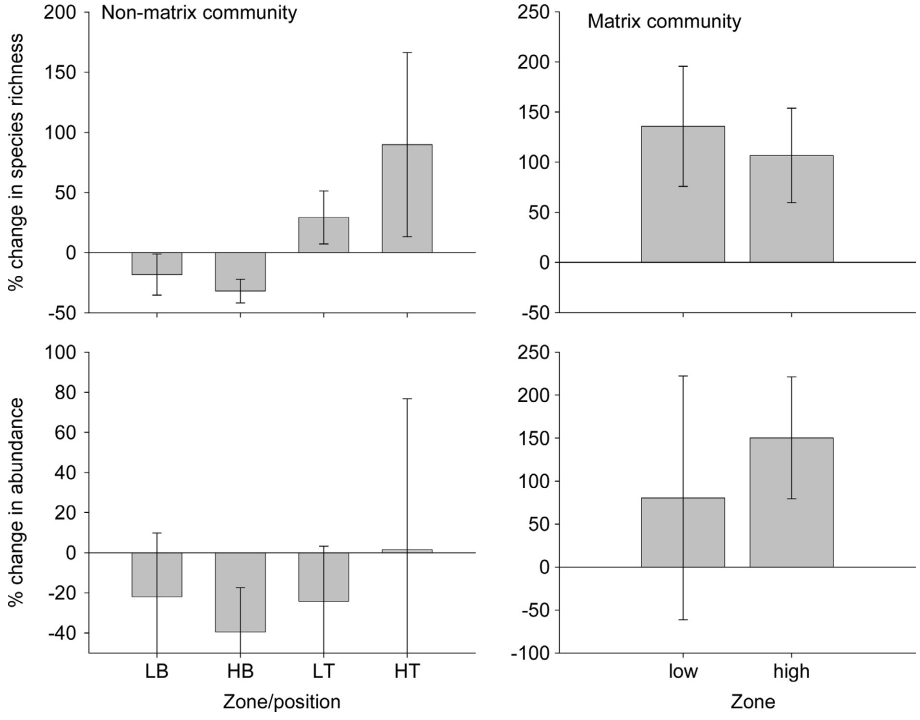

FIG. 5. Relative importance of facilitation of species richness and total abundance by serpulids for: the non-matrix community comparing between the serpulid-up (top community) and serpulid-down (bottom community) boulders relative to bare boulders and, the community within the serpulid matrix comparing between the top of boulders and the less stressful bottom of boulders. Plots show the mean percentage change ± confidence intervals in species richness or abundance. Abbreviations: LB (low zone/bottom of boulder), HB (high zone/bottom of boulder), LT (low zone/top of boulder), HT (high zone/top of boulder).

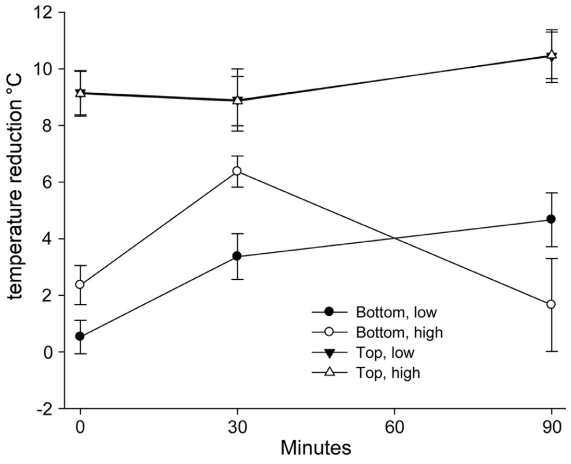

FIG. 6. Mean (±SE) reduction in temperature due to the presence of serpulids on boulders measured over 90 min. The plot shows the difference in temperature between boulders with vs. without serpulids for the top and bottom of boulders in the high and low zones at three times. For the top of boulders, symbols for both zones overlay each other.

DISCUSSION

Our experiment revealed very different communities were associated with the different types of boulders, especially in relation to the presence and position of the ecosystem engineering serpulids and also across zones. These differences were strongly influenced by communities on the top of the boulders where both species richness and total invertebrate abundance differed among boulder type. Most notably in the high zone, boulders with serpulids on the top had approximately double the species richness compared to boulders lacking serpulids and, within the serpulid matrix itself there was approximately double the species richness of small invertebrates when serpulids were on the top of boulders compared to when they were on the bottom. These results are consistent with the model of facilitation increasing in importance as environmental stress increases (greater facilitation on the top vs. bottom of boulders and, in the high vs. low zones). However, the facilitation did vary according to which part of the community was considered: species richness but not total abundance increased with increasing stress for the community external to the matrix, but within the matrix both richness and abundance (although only the high zone for abundance) increased. Moreover, the large reduction in temperature by the serpulid matrix on the top of boulders highlights a key role for modification of the abiotic environment in determining the community-wide facilitation.

Facilitation across environmental gradients

The large facilitative influence of serpulids on community structure is consistent to findings for other intertidal ecosystem engineers such as saltmarsh, algae, mussels, oysters and ascidians (Bruno 2000, Castilla et al. 2004, Altieri et al. 2010, Silliman et al. 2011, Wright et al. 2014, McAfee et al. 2016). However, we still know little about how facilitation of marine communities varies across environmental gradients. Intertidal seaweed can have strong facilitative effects on understory species in more stressful high zones (Bertness et al. 1999, Watt and Scrosati 2013) while salt marsh plants (primarily *Spartina patens*) facilitate forb seedlings in more stressful salt environments but not in lower saline marshes (Crain 2008). Conceptual models (Bruno et al. 2003) and numerous empirical studies from terrestrial systems (Callaway et al. 2002, Brooker et al. 2008) similarly suggest that the strength of facilitation increases with increasing environmental stress. The stronger facilitation of species richness by serpulids in the more stressful environment of the top of boulders is consistent with this idea. On a warm day at our site, the tops of boulders without serpulids were up to 10°C hotter than the bottom of boulders with communities in the high zone exposed to the air and subsequent emersion stresses for 2–3 h longer during daytime low tides.

The positive effects of serpulids on the top of the boulders were further demonstrated by the abundance of smaller species living within the matrix itself. Several species were only found in the serpulid matrix on the top of boulders and, in the high zone, both species richness and total invertebrate abundance within the matrix was approximately double that of the less stressful bottom of boulders. In a larger scale example of community-wide facilitation, a whole community of small intertidal invertebrates is facilitated by mussel beds over 2,100 km of the Argentinian coast (Silliman et al. 2011). In those very harsh conditions, nearly all species in the community were dependent on mussels and facilitation was consistent across intertidal zones despite lower desiccation stress in the low zone. Similarly, although we found differences in some community metrics between zones, our estimates of the relative importance of facilitation did not change across zones except for the abundance of small invertebrates within the serpulid matrix, which had a higher relative facilitation in the high zone.

Amelioration of thermal and desiccation stress are important mechanisms underpinning the facilitation of intertidal communities (Altieri et al. 2007, Silliman et al. 2011, Wright et al. 2014). Our finding of strong facilitation by serpulids on the top of boulders in the high zone and low facilitation beneath boulders in the low zone reflected temperature changes across those gradients. Although temperature was lower in the presence of serpulids on both the tops and bottoms of boulders, the bottom of boulders are shaded and cooler compared to the tops. When ambient air temperatures were >25°C, the serpulid matrix on the top of boulders reduced temperatures by at least 9°C compared to bare boulders. This reduction in temperature may be due to the color of the serpulids tubes compared to the dark color of the rocks: white artificial surfaces in the intertidal can be >5°C cooler than dark surfaces (Lathlean and Minchinton 2012). However, the structured matrix formed by the

serpulid tubes, which may retain water and reduce evaporation, may also reduce temperature. The cooler conditions within the matrix appear particularly important for small invertebrates such as the small mussel *Limnoperna* and small mobile invertebrates that were common in the matrix on the top of boulders. Many intertidal invertebrates, including mussel larvae, are susceptible to high temperatures and desiccation (reviewed in Lathlean and Minchinton 2012). The finding that *Limnoperna* only occurred on the top of boulders indicated a preference for that surface but the absence of mussels on the top of bare boulders highlights an additional dependency on serpulids. That dependency may be in response to reduced temperature of the serpulid matrix, a preference for a complex structure for attachment (Gribben et al. 2011) or passive settlement (Harvey and Bourget 1997). Mobile species living within the matrix were dominated by small *Onchidella* and polychaetes (84% of all mobile species in the matrix). Both are soft-bodied invertebrates and may find refuge from desiccation within the serpulid matrix or alternatively, the many small interstitial spaces and crevices may provide refuge from predation.

Although we did not separate the facilitative effects of mussels over and above that provided by serpulids, the presence of *Limnoperna* in the serpulid matrix may result in additional facilitation on the top of boulders and/or lead to a facilitation cascade (Altieri et al. 2007). Mussel shells provide a surface for attachment as well as additional habitat in the interstitial spaces between their shells (Altieri et al. 2007, Bateman and Bishop 2017). *Limnoperna* also accumulate sediment in their byssal threads creating habitat for small infaunal species such as the bivalve *Lasaea*.

In contrast to the facilitation on the top of boulders, beneath boulders, species richness and total invertebrate abundance did not differ between zone or boulder type, even though the overall community structure did. Previously we have shown that over 6 weeks, the presence of serpulids increased the recruitment of intertidal invertebrates (both richness and abundance) beneath boulders positioned in the low zone (Wright et al. 2016) but the findings from this current study suggest that short-term effect is not maintained. This may reflect the small size of the interstitial spaces within the serpulid matrix that would most strongly benefit larvae and small recruits but also highlights the role of numerous other processes (e.g., competition and predation) that will act over longer timescales to influence community structure. For example, the small whelk, *Haustrum*, was largely restricted to the serpulid matrix and was more common on the bottom of boulders. *Haustrum* eat a variety of small invertebrates including *Limnoperna* (Freeman et al. 2013) and the facilitation of intermediate predators may contribute to the lower species richness and abundance on the top of serpulid-down boulders if they move from the bottom to tops of boulders to forage. In addition, some species, especially grazers, were more abundant in the absence of serpulids. The gastropod *Nerita* was more abundant on the top of boulders without serpulids in the low zone. Similarly, the chiton *Sypharochiton* was abundant on the bottom of boulders without serpulids. Grazers such as *Nerita* and *Sypharochiton* feed by scraping microalgae off the rock surface with their radula and the presence of serpulids may have negative indirect effects on grazers by limiting the development of microalgal films on boulders. The apparent inhibition of species richness and abundance beneath boulders by serpulids in the high zone (Fig. 5) and the higher richness (combined) and abundance (top community) on bare boulders compared to serpulid-down boulders further supports the idea of boulders without a serpulid matrix benefitting certain species. However, because bare boulders were unintentionally smaller than serpulid-down boulders some of these differences may reflect a crowding effect on bare boulders. In addition, although our experiment only ran for 12 months and there may have been different results if the experiment went for a longer time our results are comparable to natural communities sampled beneath unmanipulated boulders at this site: species richness: 0.005 ± 0.001 cm^{-2}; abundance: 0.095 ± 0.010 cm^{-2} (N = 10, 0.5 × 0.5 m quadrats, J. T. Wright, S. Latzel, P. E. Gribben, *unpublished data*).

Disturbance and legacy facilitation by ecosystem engineers

Disturbance and subsequent movement of the ecosystem engineering serpulid created opportunities for facilitation in a different, more stressful environment – the tops of boulders, and this facilitation was strongest in the high zone. Moreover, the strong facilitation on the tops of boulders appears linked to modification of the abiotic environment and/or provision of a surface for attachment by the serpulid matrix. Although the serpulids died, the facilitation occurred via a legacy effect whereby the abiotic modification persisted after the death of the engineer (Jones et al. 1994, Hastings et al. 2007) allowing a community to persist that would otherwise be unable to survive in the harsher conditions of the tops of boulders. Similarly, the legacy effects of dead oyster shells result in abiotic modification that creates conditions that benefit oyster recruits (Lenihan 1999) and a greater abundance of epifauna, possibly due to the provision of more interstitial spaces which provide greater refuge from predation or a larger surface area for attachment compared to live oyster shells (Gutiérrez et al. 2003, Summerhayes et al. 2009). In addition, dead barnacle shells harbour a higher abundance of the gastropod *Littorina plena* which is most likely due to the higher relative humidity inside the empty tests (Harley and O'Riley 2011). Given many marine ecosystem engineers have hard calcareous shells, tubes or skeletons that are left intact after the death of the organism or colony that constructed them, this legacy ecosystem engineering may be long lasting (Gutierrez and Iribarne 1999) and common in many marine systems.

Our experiment also suggests that disturbance can enhance community structure by moving a facilitating ecosystem engineer to a new place where the relative importance of facilitation is higher. Although our experiment did not cover the full tidal range in this system, it would be valuable to understand whether the relative importance of facilitation continues to increase as environmental stress increases (e.g., increasing emersion time with tidal height), or whether a stress threshold is reached where facilitators are unable to ameliorate extreme conditions strongly enough for associated communities (Holmgren and Scheffer 2010, He and Bertness 2014). Moreover, more frequent disturbance to boulders that might occur at more wave-exposed sites may result in damage to or removal of the ecosystem engineer and negative effects on facilitated species. Understanding the influence of variable disturbance regimes for facilitated communities will also be important.

Ecosystem engineers that provide novel habitat in harsh environments can be hugely influential in determining community structure and productivity (Bruno 2000, Altieri et al. 2010, Silliman et al. 2011). There are many examples of ecosystem engineers influencing secondary succession via facilitation following a disturbance (e.g., (Farrell 1991, Bertness and Shumway 1993). We have shown that a relatively small ecosystem engineer can have large effects on community structure via facilitation and the strongest facilitation occurred following the disturbance and movement of the engineer to a more stressful environment. Our findings are consistent with the predictions from environment-stress models that facilitation can increase the density and distribution of species in stressful environments by reducing abiotic stress (Bruno et al. 2003). Moreover, we highlight how disturbance and movement of an ecosystem engineer to a stressful environment provides new opportunities for facilitation to occur.

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